Pseudothyone levini, a new species of sea cucumber (Echinodermata: Holothuroidea) from the northeastern Pacific

Philip Lambert and Kathryn L. Oliver

 (PL) Natural History Section, Royal British Columbia Museum, 675 Belleville Street, Victoria, B.C., Canada, V8W 9W2;
 (KLO) 403-1631 McKenzie Avenue, Victoria, B.C., Canada, V8N 5M3

Abstract.—Pseudothyone levini, new species (Sclerodactylidae), based on 12 specimens collected between Graham Island, Queen Charlotte Islands, British Columbia and Tacoma, Puget Sound, Washington, U.S.A. in the northeastern Pacific Ocean, is described. It ranges in depth from the intertidal zone to 70 meters on rock and in mud or gravel. Body is beige or white. Podia are scattered but more numerous in the five ambulacra. Usually ten brown dendritic tentacles. *P. levini* has mostly round or oval skin ossicles with a smooth surface, a wavy margin and small holes. Another less numerous plate is larger and thicker with scalloped margins and numerous large holes. Tails of the radials on the calcareous ring are short and curved. Tentacle ossicles range from large robust, curved rods perforated at the ends, to small curved, perforated plates. *Pseudothyone levini* is compared to seven other species currently recognized in the genus.

The family Sclerodactylidae is well represented in the Northern hemisphere, primarily in the Atlantic, from shallow water to bathyal depths (Pawson 1982). Three species in two genera of Sclerodactylidae inhabit the northwestern coast of North America. *Eupentacta pseudoquinquesemita* Deichmann ranges from Alaska to Washington, and *E. quinquesemita* (Selenka) ranges from southern Alaska to southern California (Lambert 1997). *Pachythyone rubra* (H. L. Clark) is known from Monterey Bay to Los Angeles Harbor, California (Bergen 1996).

Since 1986, five new species of holothuroids have been added to the known fauna of the northeastern Pacific (Lambert 1997, 1998). Here we describe a sixth new species of sea cucumber based on material from British Columbia and Washington. The genus *Pseudothyone* is represented by three species in the Atlantic, one in the Mediterranean, one in the Persian Gulf, one in the western Pacific, and now this one in the northeastern Pacific.

Materials and Methods

Ossicle slides were prepared as in Lambert (1985) and measurements of ossicles followed the procedures described in Lambert (1998). Ossicles were sampled from the dorsal tentacles of all specimens, middorsal regions of intact specimens, and from anterior and posterior regions of partial specimens.

Results

Order Dendrochirotida Grube Family Sclerodactylidae Pawson & Fell, 1965

Diagnosis.—Body lacks a test of imbricating plates; body wall soft; ossicles small and inconspicuous. Calcareous ring complex, with paired or unpaired processes; elements of ring not composed of a mosaic of minute pieces. Tentacles 10–20. Body may be U-shaped. Calcareous ring not as massive as in the Phyllophoridae. Tube feet usually scattered in the radii and interradii, but tendency for them to be restricted to the radii (Pawson 1982).

Subfamily Sclerodactylinae Panning, 1949; restricted by Thandar (1989).

Diagnosis.—Tentacles 10. Calcareous ring compact, short, tubular, with the radial and interradial plates fused for most of their length; posterior paired processes of the radial plates of medium length, usually broken into a few large pieces of calcite; rarely, processes unbroken.

Type genus: Sclerodactyla Ayres.

Pseudothyone Panning, 1949

Diagnosis.—Tentacles 10. Calcareous ring undivided; radialia with medium length forked-tails, which are solid or in a few large pieces. Skin ossicles consist entirely of plates.

Type species: *Pseudothyone raphanus* Düben & Koren, 1846

Pseudothyone levini new species Figs. 1-3

Diagnosis.—Ten equal tentacles. Body cylindrical; length to 140 mm. Podia scattered but more numerous and regular in the ambulacra. Majority of skin ossicles thin, round smooth plates, with smooth wavy edges and a few small holes. Less common are round to oval plates with scalloped margins and many large perforations. Tentacle ossicles range from small curved, lacy perforated plates with scalloped margins to large, heavy curved rods. Radials of calcareous ring with short curved posterior processes; posterior edge of interradials concave; radials and interradials about three times longer than wide.

Material examined.—Twelve specimens from nine localities. Material borrowed from: California Academy of Sciences (CASIZ), Canadian Museum of Nature (CMNI), Friday Harbor Laboratories (FHL), and the Royal British Columbia Museum (RBCM). Depths in meters.

Holotype.—RBCM 999-475-1, collected by Andy Lamb with aid of SCUBA, 13 Nov 1999, length 14 cm, female.

Type locality.—Point Defiance, Tacoma, Washington, USA, 47°18.4'N, 122°30.8'W, 12 m, muddy sand.

Paratypes.---RBCM 990-393-22, collected by F.W. Schueler, 4 Feb 1989, British Columbia, Queen Charlotte Islands, Graham Island, Jungle Beach, 3 km south of Lawnhill, intertidal, 1 specimen, 3 cm long. RBCM 984-223-1, collected by D.B. Quayle, 8 May 1961, British Columbia, Queen Charlotte Islands, Hecate Strait, Burnaby Narrows, 52°20.4'N, 131°20.4'W, intertidal, 1 specimen, length 8.0 cm, male. RBCM 980-343-20, collected by P. Lambert, 6 Jul 1980, British Columbia, Kyuquot Sound, Rugged Point Light, 49°58.3'N, 127°15'W, <20 m on rock, 1 specimen, 11 cm long, male. RBCM 978-315-19, collected by P. Lambert, 26 Oct 1978, British Columbia, Gulf Islands, Prevost Passage, 48°43'N, 123°20'W, 55-64 m in gravel, 1 specimen, 12 cm long, male. FHL 819, collected by S. Van Neil, 13 Aug 1964, Washington, Orcas Island, Potato Patch [local name], 48°34.9'N, 122°50.8'W, 40-55 m, 1 specimen, length 9 cm, female. CASIZ 057397, collected by Mr. and Mrs. Oldroyd, Jul 1917, Washington, San Juan Island, Friday Harbor, 48°32.7'N, 123°0.2'W, est. 46-110 m, 1 specimen, length 4.5 cm, male. RBCM 996-193-1, collected by A. Lamb, 4 Jul 1996, Washington, San Juan Island, Friday Harbor, 48°32.6'N, 123°0.7'W, 12-18 m in soft mud, 1 specimen, length 9 cm, male.

Other material.—RBCM 975-34-3, collected by John Fleury, 15 Aug 1962, British Columbia, Queen Charlotte Islands, Houston Stewart Channel, 52°6.7'N, 131°8.2'W, 30 m in gravel, 1 partial specimen, 1 cm posterior end. CMNI 1980-2097, collected by N.A. Powell, 17 Jul 1967, British Columbia, Vancouver Island, Strait of Geor-



Fig. 1. Holotype of *Pseudothyone levini* collected by Andy Lamb from a mud bottom near Point Defiance, Tacoma, Washington, USA.

gia, Nanoose Bay, $49^{\circ}15.3'$ N, $124^{\circ}8.0'$ W, 19–24 m, in gravel, 2 partial specimens, anterior end 3.5 cm and posterior end 2 cm long. CMNI 1980-2192, collected by N.A. Powell, 18 Aug 1967, Nanoose Bay, dredged parallel to the north end of the harbor, $49^{\circ}15.6'$ N, $124^{\circ}10.0'$ W, 9-15 m in gravel, 3 partial specimens, 4 cm anterior end, two posterior ends 2.4 cm and 3.4 cm long. CMNI 1980-2107, collected by D. Popham, Aug 1967, British Columbia, Haro Strait, Moresby Island, $48^{\circ}45.0'$ N, $123^{\circ}20.4'$ W, assumed to be a D.V. Ellis Station, 70 m, 1 specimen, anterior piece 3 cm long.

Description.—Body cylindrical, tapering gradually to posterior. Length of eight preserved specimens, 3–14 cm (Holotype 9 cm) with soft fleshy skin. In alcohol, skin yellowish white, flesh slightly darker. No obvious difference in color of ventral and dorsal surfaces. Tentacles white to dark brown. Living holotype beige with dark brown tentacles and purplish introvert (Fig. 1). Ambulacral podia in five regular quadruple rows and also thinly scattered be-

PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON

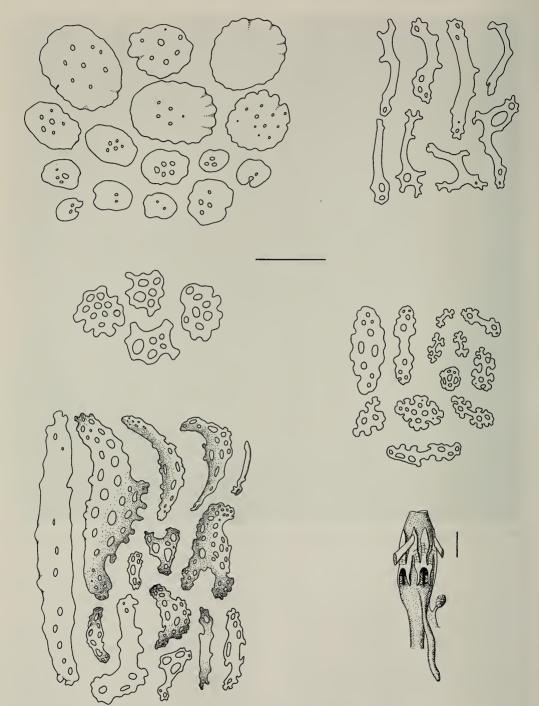


Fig. 2. Top left: typical small-holed skin ossicles. Top right: supporting rods from podia. Mid left: largeholed skin ossicles. Mid right: plates and branched rods of the introvert. Bottom left: rods and plates from tentacles. Bottom right: calcareous ring, madreporte and polian vesicle. Upper scale = $100 \mu m$. Lower right scale = 5 mm.



Fig. 3. Known distribution of *Pseudothyone levini* based on museum records.

tween the ambulacra. Podia usually flush with the skin surface in preserved specimens.

Ten dendritic tentacles; usually equal; encircling the mouth. Eight specimens have ten equal tentacles; two have eight equal and two small ventral tentacles; and one has nine equal tentacles. Two small tentacles of one specimen white, eight larger tentacles brown.

One polian vesicle in holotype, from zero to four in others. Usually one madreporite, but one specimen had a stone canal attached near calcareous ring and a second one posterior to that. Madreporite suspended in the dorsal mesentery (Fig. 2) but varying in position between the midpoint of the calcareous ring and 15 mm posterior to the tips of the ring. Madreporic body ranging from globular and furrowed, as in holotype, to oblong and smooth. Mean length of madreporic body 1.9 \pm 0.6 mm, width 1.2 \pm 0.4 mm.

Radialia with short posterior processes; some are solid but others in small pieces. Other parts of calcareous ring variably solid or in pieces. Posterior edges of the interradials concave. Radials and interradials about three times longer than wide (Fig. 2). Immediately posterior to each interradial, all specimens have a characteristic depression or pit in the membrane (Fig. 2).

Five retractor muscles attach to body wall at one third of body length from anterior end. Holotype has wide, entire retractors; in two specimens, all the retractors split longitudinally; in one specimen, one of the five retractors is split. Gonad two tufts of simple unbranched tubules, one on each side of dorsal mesentery. Each respiratory tree Y-shaped; dorsal branch often extending as far as the tentacle bulb; ventral branch shorter. Base of trees join cloaca on each side of intestinal attachment.

Generally two types of plates in skin. Commonly thin, round plates with smooth wavy margins and a few small holes; mean length 57 \pm 22 µm (*n* = 367); Holotype 65 \pm 11 (n = 40); width 42 \pm 15 µm, Holotype 50 \pm 8; mean number of holes 4 \pm 2, Holotype 4 ± 1 with a maximum diameter of 6 \pm 4 μ m, Holotype 10 \pm 3 (Fig. 2). Holes appear to get smaller with age, and some plates have none. Another type of plate, more common in smaller animals, round to oval and thick, with large holes and scalloped margins; mean length 80 \pm 27 μ m (n = 147); width 56 ± 17 μ m; mean number of holes 6 ± 3 , with a maximum diameter of $13 \pm 5 \ \mu m$ (Fig. 2) Holotype has none of this type. Tentacular ossicles range from small, lacy perforated plates to large rods. Small perforated plates curved, with scalloped margins; vary from oval to triangular with mean length of 90 \pm 60 μ m (n = 240), Holotype 84 ± 20 (n = 40); width 39 \pm 22 μ m, Holotype 35 \pm 13, mean number of holes 9 ± 7 , Holotype 13 \pm 5, with a maximum diameter of 16 \pm 7 μ m, Holotype 15 ± 5 (Fig. 2). Tentacular rods follow the circumference of the tentacle, thus vary in size, depending on location. Also, depending on orientation when viewed, they may appear narrow and curved with a few holes, or wide and heavy with many perforations (Fig. 2). Mean length of tentacular rods 212 \pm 123 μ m (n = 280), Holotype 241 \pm 108 (n = 40).

	PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
P. sculponea Cherbonnier, 1958	In sand, cobble or gravel from off Bla- nes, NE Spain in Mediterra- nean, edge of shelf (?200 m) and 83 m in Adriatic Sea (Froglia 1975). Up to 22 mm long by 8 mm trick. 8 equal, 2 small ventral. Small smooth plates with handles, sev- eral handles form a tube around a po- dia. Large smooth plates with 30–50 holes and scalloped edg- es at caudal end.
P. raphanus Düben & Koren, 1846	In sand or mud from Tron- dhjem Fjord to Mediterra- nean sea. 10- 1050 m (Mor- tensen 1977). Up to 60 mm (Mortensen 1977). 10 equal. Large, irregular, smooth plates with variable number of small (0.11- 0.22 mm) holes (Pan- ning 1949).
P. mosaica (Koehler & Vaney, 1910)	Arabian Sea (Daniel & Halder 1974); Persian Gulf (Koehler and Vaney); 53 firns. 12 mm long; 4.5 mm thick. Probably 10. Large round cal- careous plates that form a mosaic with podia emerg- ing.
P. furnestini Cherbonnier, 1969	In sandy mud, fine sand, gravel and pebbles from Bay of Bis- cay, 489– 1045 m (Cherbonnier 1969). About 15 mm long; 4.3 mm thick. 8 equal, 2 small ventral. Thick round to oval plates some larger and more ir- regular.
P. buccalis pallida Clark, 1938	On mud flat, collected with <i>P. buccalis</i> near Broome, W. Australia. Near low wa- ter mark (Clark 1938). 65 mm long; 15 mm thick. Same as <i>P. buc-</i> <i>calis.</i> Similar to <i>P.</i> <i>buccalis.</i>
P. buccalis Stimpson, 1855	In soft mud around rocks from Japan to Aden in the North, Port Jackson to Delagoa Bay in the south, Northern coast of Aus- tralia. Shore to 15 m (Clark 1938). Up to 110 mm long, 18–20 mm thick. J0; 3–4 small ventral. Medium thick layer of small plates with 4 central holes. Plate edged with small bumps. Strap like handle on top and bot- tom of plate. Occasionally 2 round mushroom shaped bumps in place of strap (Panning 1949).
P. belli Ludwig, 1886	Albrothos Reef, Brazil to Har- bour of Co- lon, Panama, and Torgutas, Florida. Shore to 22 m (Deichmann 1930). 8 to 50 mm. 8 equal, 2 small ventral. 1) 4 holed knobbed but- tons with 4–8 marginal knobs; 2 cen- tral knobs united by a handle. 2) plates with more holes and knobs. 3) smooth plates with several holes.
<i>P. levini</i> This paper	In mud or grav- el from the Queen Char- lotte Islands south to Puget Sound, Wash- ington. Shore to 110 m. Up to 90 mm long. I0 equal. Round plates with smooth wavy mar- gins, few small holes. Fewer large round to ir- regular, plates with scalloped margins and many large perforations.
	Distribution Dimensions Tentacles Skin ossicles

Table 1.-Distribution and morphology of all known species of Pseudothyone.

594

PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON

	<i>P. levini</i> This paper	<i>P. belli</i> Ludwig, 1886	P. buccalis Stimpson, 1855	P. buccalis pallida Clark, 1938	P. furnestini Cherbonnier, 1969	P. mosaica (Koehler & Vaney, 1910)	P. raphanus Düben & Koren, 1846	P. sculponea Cherbonnier, 1958
Other ossicles	Tentacles: small, curved, perfo- rated plates with scalloped margins. Rods range from small, thin, sharp with a frow holes to thick, heavy, long, with more holes.	Tentacles: ro- settes and del- icate perforat- ed rods. Well developed end plates. Ob- long support- ing tables with rudimen- tary spire. (Defmann 1930) and		Tentacles and introvert: without ro- settes but many slender rods, with few holes, or holes at ends. (Clark 1938).	Tentacles: rods with wide perforated ends. No sup- porting rods in podia; rudi- mentary end- plate; Intro- vert: rods with scalloped edges, and small plates.	Supporting ta- bles in podia.		Tentacles: rods up to 700 µm long, and ro- settes. No os- sicles in podia except end- plate with ra- diating spokes.
Calcareous Ring	Radials with short curved tails. Interra- dials with concave pos- terior edge. Radials and interradials about 3× as long as they are wide.	vonuer 1710). Radials with long slender processes, cleft almost to the middle of the interradi- als. Radials and interradi- als high and narrow. Inter- radials slight- ly incised be- hind (Deichmann 1930)	Radials with long forked tails. Broad tails. Broad radials and in- terradials- merge with one another. Anterior radi- als to a point, with parallel edges. Anteri- or interradials lance shaped (Panning 1940)	Same as P. buc- calis.	Radials with medium length tails made of 5 pieces; anteri- or of radials narrow with gutterlike groove; inter- radials with flattened or pointed tips.	Radials with long tails in about 5 piec- es; radials with notch at anterior end.	Radials with rounded slen- der tip, and medium length undi- vided forked tails. Delicate. Radials and interradials broad in the middle (Pan- uing 1949).	Radials with forked tails of moderate length; trough-like groove at an- terior end; in- terradials with pointed ante- rior and curved poste- rior edge.
Other com- ments	Body cylindrical and curved.	Body slightly curved (Deichmann 1930).	Body Type Body Type indistinctly 4 or 5 angled (Theel 1886).	Pure white body, other- wise, same as <i>P. buccalis.</i>	Body short and thick; u- shaped; nar- row caudal end; podia scattered but also in rows.	Body curved and stiff with covering of plates.	Body with a long, thin 'tail'' (Mor- tensen 1977).	Caudal end without podia.

VOLUME 114, NUMBER 3

Table 1.-Continued.

595

Introvert has small branched rods or rosettes; mean length $65 \pm 23 \ \mu m$ (Fig. 2). No end plates found in podia; podia with branched rods similar to tentacles. Larger specimens have fewer ossicles in podia and skin; many have eroded edges. Deterioration is likely natural rather than due to preservatives because tentacle ossicles in the same specimen not eroded.

Etymology.—The species is named after Dr. Valery S. Levin, of the Kamchatka Institute of Fisheries and Oceanography, Petropavlovsk, Russia in recognition of his numerous contributions to holothuroid systematics and ecology.

Distribution and bathymetric range.-Collections range from Graham Island, Queen Charlotte Islands, British Columbia (53°23'N, 131°55'W) to Point Defiance, Tacoma, Puget Sound, Washington (47°18.4'N, 122°30.8'W) (Fig. 3). Depths range from intertidal to 70 meters, on rock or in mud or gravel. One record was between 46 and 110 meters but the precise depth could not be confirmed. Most specimens occurred in less than 60 meters. Andy Lamb collected two specimens from mud with the aid of SCUBA. One specimen was collected in a subtidal exposed rocky habitat from a pocket of gravel and two specimens were collected from the intertidal zone.

Discussion

The family Sclerodactylidae is morphologically intermediate between the Phyllophoridae with complex calcareous rings and the Cucumariidae with simple rings (Pawson 1966). Thandar (1989, 1990) states that several seemingly unrelated forms are included in the family, with some genera fitting equally well in the Phyllophoridae, which are characterized by long tubular calcareous rings composed of a mosaic of minute pieces. The family Sclerodactylidae currently contains three subfamilies: the 10tentacled Sclerodactylinae and Sclerothyoninae, largely Atlantic in distribution, and

the Cladolabinae found typically in the Indo-West Pacific (Thandar 1989), Pawson & Fell (1965) state that having undivided processes is the key character of Sclerodactylidae that separates it from the Phyllophoridae; however, Thandar (1989) feels that this is a poor character because even within a single species of Sclerodactylidae the processes may be divided or undivided. He prefers to emphasize the short compact nature of the calcareous ring in this family (Thandar 1989, Fig. 1b). The calcareous ring of Pseudothyone levini is compact with short curved processes. While the processes in most specimens appear to be in small pieces, some are undivided. This variability in the posterior processes and the general character of the calcareous ring agree with the subfamily Sclerodactylinae as Thandar defined it.

Table 1 compares the distribution and morphology of the new species with the seven known species of *Pseudothyone*, all of which have only plate ossicles in the body wall and generally inhabit mud in shallow water. Pseudothyone levini can be distinguished from other species of Pseudothyone by skin ossicles and the form of the calcareous ring. Pseudothyone levini of different sizes, and presumably different ages, show differences in the form of their skin ossicles as do specimens from rocky habitats versus mud. Specimens greater than 10 cm long had few of the large-holed plates found in small animals. This variability in ossicles may represent growth stages, but a more complete size series of specimens is required before the relationship of size and ossicle form can be determined. One specimen from a rocky substrate had larger small-holed skin ossicles than those from mud. Apart from the one rock-dwelling specimen the skin ossicles seemed to deteriorate in larger animals. This deterioration was unlikely a function of poor preservation as the tentacle ossicles in these specimens appeared normal.

Pseudothyone levini appears to be most closely related to P. raphanus (Düben &

Koren, 1846) from the North Atlantic. The skin ossicles of P. raphanus are a single type of perforated plate with large holes. Pseudothyone levini has a few large-holed perforated plates like the former but the dominant ossicles of mature specimens are smooth, rounded plates with small holes. The curved body of P. raphanus has an expanded anterior part and long slender caudal portion while P. levini is curved but only slightly tapered. Pseudothyone raphanus lives in soft substrates with its tail protruding and ingests the bottom material directly according to Mortensen (1977). On a night dive, Andy Lamb observed the tentacles of Pseudothvone levini extended above the mud surface presumably feeding on suspended particles. He collected one specimen and saw several other individuals in the same posture. On a second dive at the same location during daylight, none were seen. Several dredged specimens consist of only anterior and posterior portions, suggesting that the animal assumes a Ushaped position with anterior and posterior ends at the surface or protruding from the sediment.

Four *Pseudothyone* species have calcareous rings with long posterior processes, three have medium length tails, and *P. levini* has short curved tails.

Unlike most specimens examined, two possessed small ventral tentacles. We speculate that these may have been regenerating after an injury or in the case of the 3-cm specimen, may be a juvenile characteristic, but more specimens would be required to determine this. Tentacle sizes among the species of this genus vary (see Table 1). Either this character is variable in the genus or the genus is not well characterized and needs to be revised. We assume that variations in the shape of the retractor muscles are artifacts that may have been caused by sudden contractions during preservation.

Acknowledgments

Thanks to Andy Lamb of the Vancouver Aquarium for his keen eyes in detecting unusual species and for collecting two specimens that helped us to complete the description started a few years ago. The paper was improved by the constructive criticisms of Dr. Alex Kerr and one anonymous reviewer. The authors thank the Director of the Royal B.C. Museum for research funding and for supporting one of us (KO) during a University of Victoria Co-op work term in the fall of 1997 when the initial work on this new species was done.

Literature Cited

- Bergen, M. 1996. Chapter 9. Class Holothuroidea. Including keys and descriptions to all continental shelf species from California. Pp. 195–250 in J. A. Blake, P. H. Scott, & A. Lissner, eds., Taxonomic atlas of the benthic fauna of the Santa Maria Basin and the Western Santa Barbara Channel, Santa Barbara Museum of Natural History, Santa Barbara, 305 pp.
- Cherbonnier, G. 1958. Note sur *Pseudothyone sculponea*, nouvelle espece d'holothurie Dendrochirote de Mediterranee.—Vie et Milieu 9:62–66.
- . 1969. Echinodermes recoltes par la Thalassa au large des cotes ouest de Bretagne et du Golfe de Gascogne (3–12 Aout 1967).—Bulletin du Museum National d'Histoire Naturelle, Paris, 4e serie 41:343–361.
- Clark, H. L. 1938. Echinoderms from Australia an account of collections made in 1929 and 1932.—Memoirs of the Museum of Comparative Zoology at Harvard College 55:1–596.
- Daniel, A., & B. P. Halder. 1974. Holothuroidea of the Indian Ocean with remarks on their distribution.—Journal of the Marine Biological Association of India 16:412–436.
- Deichmann, E. 1930. The holothurians of the western part of the Atlantic Ocean.—Bulletin of the Museum of Comparative Zoology (Harvard) 71: 43–226.
- Düben, M. W., von., & J. Koren. 1846. Ofversigt af Skandinaviens Echinodermer.—Kungliga Svenska Vetenskaps-Akademiens Handlingar for 1844:229–328.
- Froglia, C. 1975. Segnalazione di *Pseudothyone sculponea* Cherbonnier nell'Adriatico (Echinodermata, Holothuroidea).—Annali del Museo Civico di Storia Naturale Giacomo Doria 80:259– 262.
- Koehler, R., & C. Vaney. 1910. Description d'holothuries nouvelles appartenant au Musee Indien.—Records of the Indian Museum, Calcutta 5:89–104.

- Lambert, P. 1985. Geographic variation of calcareous ossicles and the identification of three species of eastern Pacific sea cucumbers (Echinodermata: Holothuroidea). Pp. 437–443 in B. F. Keegan & B. D. S. O'Connor, eds., Echinodermata: Proceedings of the Fifth International Echinoderm Conference, Galway, A.A. Balkema, Rotterdam, 662 pp.
- - —. 1998. Pentamera rigida and Pentamera pediparva, two new species of sea cucumber from the west coast of North America (Echinodermata: Holothuroidea).—Proceedings of the Biological Society of Washington 111:535–550.
- Ludwig, H. 1886. Die von G. Chierchia auf der Fahrt der Kgl. Ital. Corvette "Vettor Pisani" gesammelten Holothurien.—Zoologiscen Jahrbüchern. Zeitschrift für Systematik, Geographie und Biologie der Thiere 1886:1–36.
- Mortensen, T. 1977. Handbook of the echinoderms of the British Isles. Dr. W. Backhuys, Uitgever, Rotterdam, 471 pp.
- Panning, A. 1949. Versuch einer Neuordnung der Familie Cucumariidae (Holothurioidea, Dendrochirota).—Zoologische Jahrbücher Abteilung für

Systematik, Oekologie und Geographie der Tiere 78:404–470.

- Pawson, D. L. 1966. Phylogeny and evolution of holothuroids. Pp. 641–646 in R. C. Moore, ed., Treatise on invertebrate paleontology, Part U, Echinodermata 3, vol. 2, Geological Society of America and University of Kansas Press, Lawrence, 1027 pp.
- . 1982. Holothuroidea. Pp. 813–818 in S. P. Parker, ed., Synopses and classification of living organisms, McGraw-Hill, Toronto, 1232 pp.
- —, & H. B. Fell. 1965. A revised classification of the Dendrochirote Holothurians.—Breviora 214:1–7.
- Sluiter, C. P. 1910. Westindische Holothurien.—Zoologische Jahrbuecher Jena Suppl. 11:331–342.
- Stimpson, W. 1855. Descriptions of some new marine invertebrata. Philadelphia. 10 pp.
- Thandar, A. S. 1989. The sclerodactylid holothurians of southern Africa, with the erection of one new subfamily and two new genera (Echinodermata: Holothuroidea).—South African Journal of Zoology 24:290–304.
- ——. 1990. The phyllophorid holothurians of southern Africa with the erection of a new genus.— South African Journal of Zoology 25:207–223.
- Theel, H. 1886. Report on the Holothurioidea dredged by the HMS Challenger during the years 1873– 1876 Part II. Voyage of the HMS Challenger-Zoology, vol. XIV, Part 39.